Induction of gravity-dependent plasmatic responses in root statocytes by short time contact between amyloplasts and the distal endoplasmic reticulum complex *

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Abstract. Statocytes from roots of Lepidium sativum L., which developed after a 2-min soaking on a horizontal clinostat (2 rotations per min) for 44 h, exhibit the same polarity as in vertically grown roots, as indicated by a complex of endoplasmic reticulum (ER) cisternae at the distal cell pole. Amyloplasts are distributed randomly. The kinetics of graviresponse (= curvature) of such roots are identical to those of normally grown roots. Ten-minute exposure of the root, after 24 h development on the clinostat with gravity acting towards the root's basis (inversion), induces no changes in statocyte ultrastructure. However, corresponding exposure in normal orientation leads to subsequent disintegration of the distal ER complex, loss of amyloplast starch, confluence of lipid droplets, and an increase of the lytic compartment. These ultrastructural events thus appear to be induced by a physical contact – however short – between amyloplasts and the distal ER complex.

Key words: Amyloplast – Endoplasmic reticulum – Gravity perception – Lepidium – Statocyte.

Introduction

Rotating 24-h-old, vertically grown roots of Lepidium on a horizontal clinostat (2 rotations per min) for an additional 20 h leads to an “ultrastructural response” restricted to the statocytes (Hensel and Sievers 1980). The single responses of the individual roots vary qualitatively and quantitatively but the loss of cell polarity and certain parameters are most obvious: disintegration of the distal endoplasmic reticulum (ER) complex; loss of amyloplast starch; confluence of lipid droplets; early development and increase of the lytic compartment; and even lysis of anticlinal cell walls. Finally, statocytes respond to prolonged omnilateral gravi-stimulation by self-destruction (Hensel and Sievers 1980). If, on the other hand, seeds of Lepidium germinate and their primary roots grow on a continuously rotating clinostat, such an ultrastructural response of statocytes does not occur (Sievers et al. 1976).

The different ultrastructural aspects resulting from these two treatments cannot be sufficiently explained by mere physical effects. In either case the gravity vector acts perpendicular to the length axis of the root, changing its direction continuously during rotation. While the physical parameters are the same in both treatments, the physiological preconditions are completely different: In case of prior vertically grown roots, rotation acts on already differentiated statocytes with amyloplasts sedimented on the distal ER complex. These statocytes are able to perceive gravity (Sievers and Volkmann 1972; Volkmann and Sievers 1979), also causing at least the ultrastructural response of these cells. The polarity of the root statocytes does not occur in the dry embryonic radicle; it develops during soaking and germination of the seed (Volkmann 1976; Friedrich 1978). In roots germinating on a clinostat, differentiation of statocytes thus takes place during the rotation. In this case the polarity of the statocytes is also developed in spite of rotation both on slow and fast rotating clinostats (Sievers et al. 1976). However, the well-developed amyloplasts never sediment on the distal ER complex.

As the clinostat is proved to be a non-stimulus-free treatment to differentiated statenchymas (Elfving 1883; Larsen 1962; Hensel and Sievers 1980), the aim of this study is to evaluate the physiological significance of clinostat rotation to differentiating statenchymas. In particular, we investigated whether an
even short time sedimentation of amyloplasts on the distal ER complex is sufficient to induce an ultrastructural response of statocytes during an additional prolonged rotation on a clinostat.

**Material and methods**

Seeds of *Lepidium sativum* L. were soaked in distilled water for 1-2 min, just sufficient time to develop a slime sheath, and placed in plant chambers mounted on a clinostat (see Hensel and Sievers 1980). Rotation of the clinostat was started immediately afterwards. The seeds were oriented in such a manner that the roots grew out parallel to the horizontal axis of the clinostat. After 32 h and 44 h, respectively, the roots were fixed in situ on the rotating clinostat with a 2% aqueous solution of KMnO$_4$. For further preparations see Hensel and Sievers (1980).

In other experiments the clinostat was tilted over 90° after 24 h and in this way the roots were exposed to the gravity vector for 10 min. The roots were oriented such that the gravity vector acted parallel to their length axes in the direction of the root tip (normal orientation) or in the direction of the root basis (inversion). During this vertical exposure the clinostat was switched off. After 10 min it was switched on again and tilted over 90°, the roots were then rotated for an additional 20 h with their length axes parallel to the again horizontal rotation axis. After 44 h of total rotation time, they were fixed in situ. Roots not growing parallel to the clinostat axis were discarded (50-60% of the germinated roots).

Graviresponse (curvature) was measured by stopping the clinostat, thus exposing the roots perpendicular to the gravity vector. Normal grown roots of the same age served as controls.

All experiments were performed in darkness at 26 ± 1°C, manipulations and photographic registration of the graviresponse were carried out in dim-green safelight.

**Results**

About 12 h after soaking, the primary roots of *Lepidium* break the seed coat at the micropyle. In a previous communication (Hensel and Sievers 1980) it was shown that 24-h-old, normally grown roots which were rotated for an additional 20 h on a clinostat develop the specific ultrastructural response described in the introduction.

In order to compare this effect with the germination on the clinostat, the roots were fixed after 32 h to submit the germinated roots to a rotation time of 20 h and after 44 h to get roots of the same age as in the above-mentioned experiments. As there was no difference in ultrastructure and graviresponse between these two rotation times, only the effects of 44 h of rotation are reported in the following.

_Ultrastructure of statocytes from roots germinated and grown on the clinostat (44 h)._ After 44 h of rotation the amyloplasts are randomly distributed in the statocytes, and the nucleus is situated at the proximal cell pole (Fig. 1). The ER complex at the distal cell pole is clearly developed. None of the parameters of the ultrastructural response is evident in the statocytes. The ultrastructure of the statocytes is thus the same as in the normally grown control roots (Sievers and Volkmann 1972; Hensel and Sievers 1980), except the rotation-induced random distribution of the amyloplasts.